POLLINATION POSTULATES AND TWO-DIMENSIONAL POLLINATION IN HYDROPHILOUS MONOCOTYLEDONS[1]

Paul Alan Cox[2] *and R. Bruce Knox*[3]

ABSTRACT

A set of pollination postulates are proposed to unify vector identification in pollination biology. These postulates were used to test theoretical predictions concerning two-dimensional pollination systems in Halodule, Halophila, Ruppia, Lepilaena, *and* Amphibolis. *The general syndrome of pollination on the water surface is illustrated by intertidal populations of* Amphibolis antarctica, *whose staminate flowers abscise during low spring tides and float to the surface where they dehisce, expelling a cottony mass of filamentous pollen. The pollen floats and forms search vehicles or pollen assemblages that collide with stigmas on the water surface. The search efficiency of large search vehicles was examined by video analysis of* Ruppia spiralis *pollination. Large search vehicles were found to be more likely to hit stigmas than small ones.*

Although the determination of the vectors responsible for transporting pollen from flower to flower is a central task of pollination biology, no standard criteria for vector determination exist. Historically, methodologies for vector determination range from careful ecological studies to conjecture based upon superficial examination of dried herbarium specimens or worse. As a result, the literature of pollination ecology is uneven in rigor. Perhaps since anthecology originated as a specialization of plant taxonomy, textbooks and reviews tend to favor claims with historical priority. Thus, even incorrect ideas are notoriously difficult to remove from the literature.

An example may be found in the literature concerning the pollination ecology of *Freycinetia arborea* Gaud. (Pandanaceae) in Hawaii. Pollination by rats was suggested by Degener (1930), who made no experiments or observations of pollinator visitation. No consideration was given to how *F. arborea* was pollinated before the introduction of rats to Hawaii by Polynesian colonists in 400 A.D. (Jennings, 1979). However, despite several previous detailed accounts of *Freycinetia* pollination in the Dutch, German, and English literature (see reviews in Cox, 1981, 1984), Degener's rather anecdotal sketch emerged as authoritative. Frequently cited in textbooks, but sometimes attributed to a secondary source (Proctor & Yeo, 1973), the story of rat pollination of *Freycinetia* thus began a life of its own. Each recounting of the story added to both its detail and apparent authenticity. Although the original report did not indicate the time of day that pollination supposedly occurs, this important detail later appeared in a major compendium (Faegri & van der Pijl, 1979). Degener (pers. comm.), however, never witnessed rat visitation but only inferred it from scratches on the floral bracts. Subsequent studies demonstrated such scratches to be caused by the introduced white-eyes that now pollinate *F. arborea*. Electron microscope analysis of bird specimens collected in the nineteenth century indicates that formerly pollination was mediated by now extinct honeycreepers (Cox, 1983a).

Such confusion in vector identification is reminiscent of disputes concerning pathogen determination in medicine in the 1850s. The prevailing theory was that diseases like tuberculosis are caused by a variety of climatic, environmental, and organic factors. However, Robert Koch (1880) proved that tuberculosis is caused by a single bacterium. His

TABLE 1. *Postulates.*

Koch's Postulates

1. Pathogen must be demonstrated in all cases of the disease.
2. Pathogen must be cultivated in pure culture.
3. Cultured pathogen must cause disease in healthy individuals.
4. Pathogen must be re-isolated from these infected individuals.

Pollinaton Postulates

In the field:

1. Pollen transfer from anther or pollen presentation apparatus to vector must be observed.
2. Pollen transport by vector must be observed.
3. Pollen transfer from vector to stigma must be observed.
4. Pollen deposited by vector on stigma must be demonstrated to effect fertilization.

rigorous methodology has since been encapsulated in a series of postulates named after him (Table 1). Brock (1966) and Harper (1978) have suggested that ecology could benefit from similar rigor.

Using Koch's postulates as a model, we propose a standard set of postulates for vector determination in pollination biology (Table 1). Our postulates require confirmation of each stage of the interaction between anther, vector, and stigma. We submit that unless these postulates have been met, the efficacy of a presumed vector in pollination has yet to be proven. We additionally suggest that all such determinations be made in the natural populations rather than in the laboratory, where unnatural conditions can deceive even the most careful investigators.

We used these pollination postulates to guide our studies of pollination in hydrophilous monocotyledons and to test previous theoretical predictions concerning two-dimensional pollination systems (Cox, 1983b).

THEORETICAL PREDICTIONS OF TWO-DIMENSIONAL POLLINATION SYSTEMS

The probability of a pollen grain reaching the stigma can be modeled for aquatic regimes where wind, currents, and orbital wave motion drive it along an essentially random path. In the simple case of a pollen grain tracing a Brownian path, it can be shown that the pollen grain will eventually hit any coplanar stigma, given enough time (Cox, 1983b; Hersch & Griego, 1969). However, in three dimensions there is a probability that a pollen

grain on a random trajectory will not hit any given stigma even given an infinite amount of time. Since such fractal motion is recurrent in two dimensions but not three, it was predicted that selection will favor the evolution of two-dimensional pollination systems where such systems are possible, i.e., in aquatic regimes such as ponds, and intertidal regions (Cox, 1983b).

The theoretical effectiveness of two-dimensional pollination systems can be examined through the use of search theory (Cox, 1983b; Koopman, 1956). Of particular interest are the effects of pollen morphology on stigma encounter rates. The probability P of a pollen grain encountering a fixed stigma, if the pollen grain traces a random path in the same plane, can be shown to be

$$P = 1 - e^{-wL/A}, \qquad (1)$$

where w is the width of the path swept by the pollen grain, L is the length of the search path, and A is the search area (Cox, 1983b). Hence at low encounter probabilities, even a small increase in the pollen grain diameter will result in a very large increase in probability of encountering a stigma. Of particular interest is the exponential nature of this function: at low encounter probabilities a doubling of pollen grain diameter will result in a more than two-fold increase in the probability of hitting a stigma.

From these theoretical considerations two general predictions can be made concerning hydrophily (water-pollination): 1) a 2-D pollination system will be more efficient than a 3-D system, and thus favored by natural selection if pollen and stigmas can be dispersed in the same plane; and 2) in a 2-D pollination system, pollen grains or aggregations of large dimension will be much more likely to hit stigmas than small ones. Following the nomenclature of search theory (Koopman, 1956; Cox, 1983b), such aggregations will hereafter be termed "search vehicles."

EMPIRICAL PROPERTIES OF TWO-DIMENSIONAL POLLINATION SYSTEMS

These theoretical predictions concerning two-dimensional pollination were tested in five different genera of marine and freshwater aquatic plants. In accordance with our postulates, we observed in each species the release of the pollen from the anther to the surface, transport of the pollen by the water surface, and deposition of the pollen from the water surface onto the stigma. We are currently studying the efficacy of fertilization under field conditions. Such confirmation is important
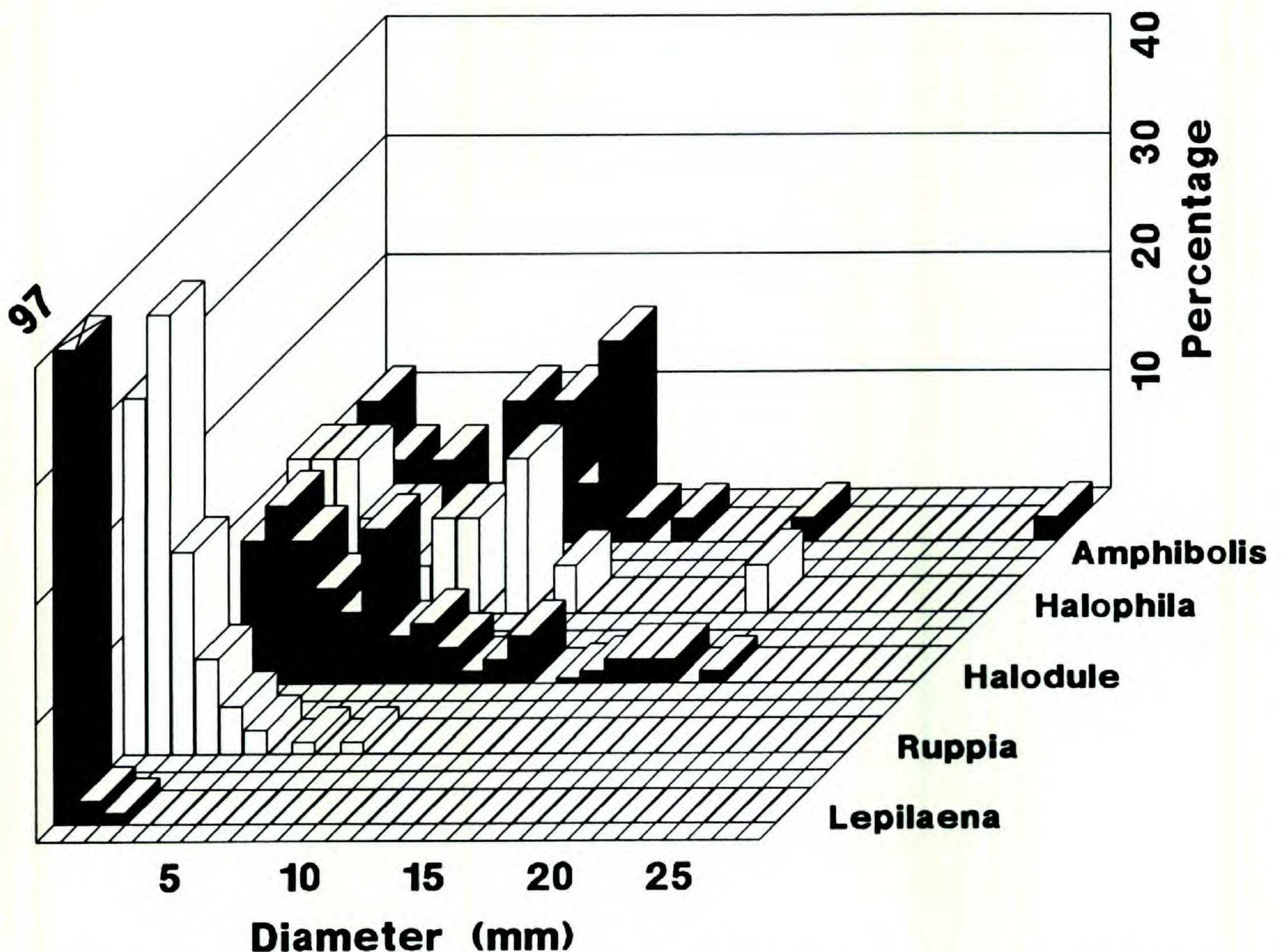
FIGURE 1. *Size distribution of floating search vehicles (pollen aggregations) from five genera of hydrophilous monocotyledons:* Halodule pinifolia *(median = 5,000 µm, N = 114)*, Halophila ovalis *(median = 8,000 µm, N = 17)*, Ruppia spiralis, Altona, Victoria, *population (median = 1,361 µm, N = 300)*, Lepilaena cylindrocarpa *(median = 338 µm, N = 172)*, *and* Amphibolis antarctica *(median = 8,500 µm, N = 40)*.

because of the possibility of apomixis in some dioecious seagrasses, such as *Halophila stipulacea* (Forsk.) Aschers. (Hydrocharitaceae), where seed has been found to develop in pistillate cultures (McMillan, 1980).

Our study focused on genera in which pollen is transported in direct contact with the water. However, plants in which pollination occurs by the collision of floating staminate flowers with buoyant pistillate flowers, such as some genera of the Hydrocharitaceae, e.g., *Vallisneria, Nechamandra, Enhalus, Lagarosiphon,* or *Appertiella,* can also be said to have in effect two-dimensional pollination systems (Cook, 1982; Ernst-Schwarzenbach, 1945; Troll, 1931; Wylie, 1917; Cox, 1988a). Taxa also exist that have submarine two-dimensional pollination systems, such as *Thalassia testudinum* Banks ex Konig (Hydrocharitaceae), where pollen is released at the substrate surface and dispersed in negatively buoyant search vehicles (Cox & Tomlinson, 1988; Cox, in press). Pollination is submarine and essentially occurs along the plane of the substratum.

In the species we studied, e.g., *Halodule pinifolia* (Miki) den Hartog (Cymodoceaceae), *Halophila ovalis* (R. Br.) Hook. f. (Hydrocharitaceae), *Ruppia maritima* L. ex Dumort (Ruppiaceae), *Lepilaena cylindrocarpa* (Koernicke ex Walp.) Benth. (Zannichelliaceae), and *Amphibolis antarctica* (Labill.) Sonder & Aschers. ex Aschers. (Cymodoceaceae), we found pollination to occur on the water surface. In these species the pollen is hydrophobic and forms floating search vehicles that collide with the buoyant stigmas. However, the search vehicles are formed differently and are of different size in each species (Fig. 1). The pollen grains of *Halodule pinifolia,* for example, are filiform and link together in search vehicles that resemble snowflakes, while the pollen grains of *Lepilaena cylindrocarpa* are small, spherical, and dispersed in a floating mat of mucilaginous slime. The pollen grains of *Halophila ovalis* are oval and

of medium size, but are dispersed in long floating mucilaginous tubes of thecal origin (Cox & Knox, 1986; Pettitt, 1980, 1981). These tubes link together to form featherlike search vehicles. *Ruppia spiralis* pollen grains have a boomerang shape, forming search vehicles by lining up side-to-side (Cox & Knox, 1986; Gamerro, 1968; Verhoeven, 1979; Van Vierssen et al., 1982). Similar evolutionary convergences can also be found in stigma morphologies: the marine genera have filamentous, smooth stigmas while the freshwater genera have small indusiate stigmas that create small depressions on the water surface. It therefore appears that there has been convergent evolution towards a surface pollination syndrome.

TWO-DIMENSIONAL POLLINATION IN *AMPHIBOLIS ANTARCTICA*

The pollination ecologies of *Halodule pinifolia*, *Halophila ovalis*, *Ruppia spiralis*, and *Lepilaena cylindrocarpa* will be reported in detail elsewhere (Cox & Knox, in press). However, many of the essential features of surface-pollinated taxa are illustrated by the pollination ecology of *Amphibolis antarctica*, a dioecious seagrass found in the waters of Western Australia, Southern Australia, Victoria, and Tasmania (Ducker et al., 1977; Aston, 1973).

Amphibolis antarctica plants produce solitary floral units (for discussions of floral terminology see McConchie et al., 1982; Tomlinson, 1982) at the ends of short lateral leafy branches with distichous phyllotaxis. The staminate floral units are bipartite, with two fused stamens borne on a short pedicel. The pistillate floral units consist of two free carpels, each with a sessile ovary bearing three slender styles (McConchie et al., 1982; Tomlinson, 1982). A few days prior to dehiscence, the pedicel bearing the staminate floral units elongates, pushing the fused anthers up from between the bracts. However, the floral units (Fig. 2A) are still hidden by the leafy shoots until they abscise and float to the surface. Within the anthers, the mature tricellular pollen grains are filamentous and 3,000–5,000 μm long, with forked tails (Ducker et al., 1978). The mature pollen "noodles" lack a developed exine (Pettitt et al., 1983). Details of pollen–stigma interactions and pollen tube growth have been investigated by Pettitt et al. (1980, 1983). In pistillate plants the mature styles protrude from the shoots in a plane orthogonal to the plane of phyllotaxis.

Pollination in *Amphibolis antarctica* has been described as submarine, i.e., occurring beneath the surface of the water (Ducker et al., 1978; Pettitt et al., 1980, 1981, 1983). However, the possibility of variation is indicated by previous observations that the male flowers may be shed, releasing their pollen on the surface of the sea, with the floating pollen forming large aggregates (Ducker et al., 1978).

We studied the pollination ecology of *Amphibolis antarctica* in an intertidal population at Point Lonsdale, Victoria, Australia, attempting to verify each of the previously discussed pollination postulates. At 3:04 P.M. on December 13, 1986, during a low (0.3 m) tide, numerous staminate and pistillate plants in the population were examined and found to have mature flowers. At low tide, the tops of the plants were observed floating on the surface, with the plane of the distichous phyllotaxis coplanar with water surface. As a result, one set of stigmas from each pistillate floral unit penetrated the water surface. A few abscised staminate flowers that had already released their pollen were found along the beach, but no pollination events were observed.

Between 4:40 P.M. and 5:20 P.M. on December 15, 1986, during an even lower tide (0.2 m), several thousand staminate floral units were observed to abscise (Fig. 3A) and float to the surface (Fig. 3B). Once on the surface, the anthers dehisced longitudinally and extruded flocculent masses of floating pollen (Figs. 2A, 3C). The pollen mass from each male floral unit rapidly expanded on the water surface into large floating search vehicles (median diameter = 8,500 μm, N = 40) of fractal geometry (Fig. 3D). The tops of nearly all of the mature pistillate plants in the population were exposed during this extremely low tide so that one set of stigmas in each floral unit penetrated the water surface (Fig. 3E). Pollination was observed to occur on the water surface through the collision of the floating search vehicles with the stigmas (Figs. 2B, 3E). As the tide came back in, thousands of empty staminate floral units were washed up along the beach. Field experiments with mature and slightly immature pollen showed mature pollen to float, while slightly immature pollen proved to be neutrally buoyant.

By observing actual pollination events at the water surface, we can with confidence ascribe a two-dimensional surface pollination syndrome to *Amphibolis antarctica*. Two-dimensional surface pollination is probably characteristic of *A. amphibolis* in the intertidal zones where the stigmas have the potential to be exposed during low tides. The species can grow and flower at greater depths, however, where pollination, if it occurs at all, must of necessity be submarine. Although we believe *Amphibolis antarctica* to be primarily surface-pollinated, submarine pollination cannot be ex-
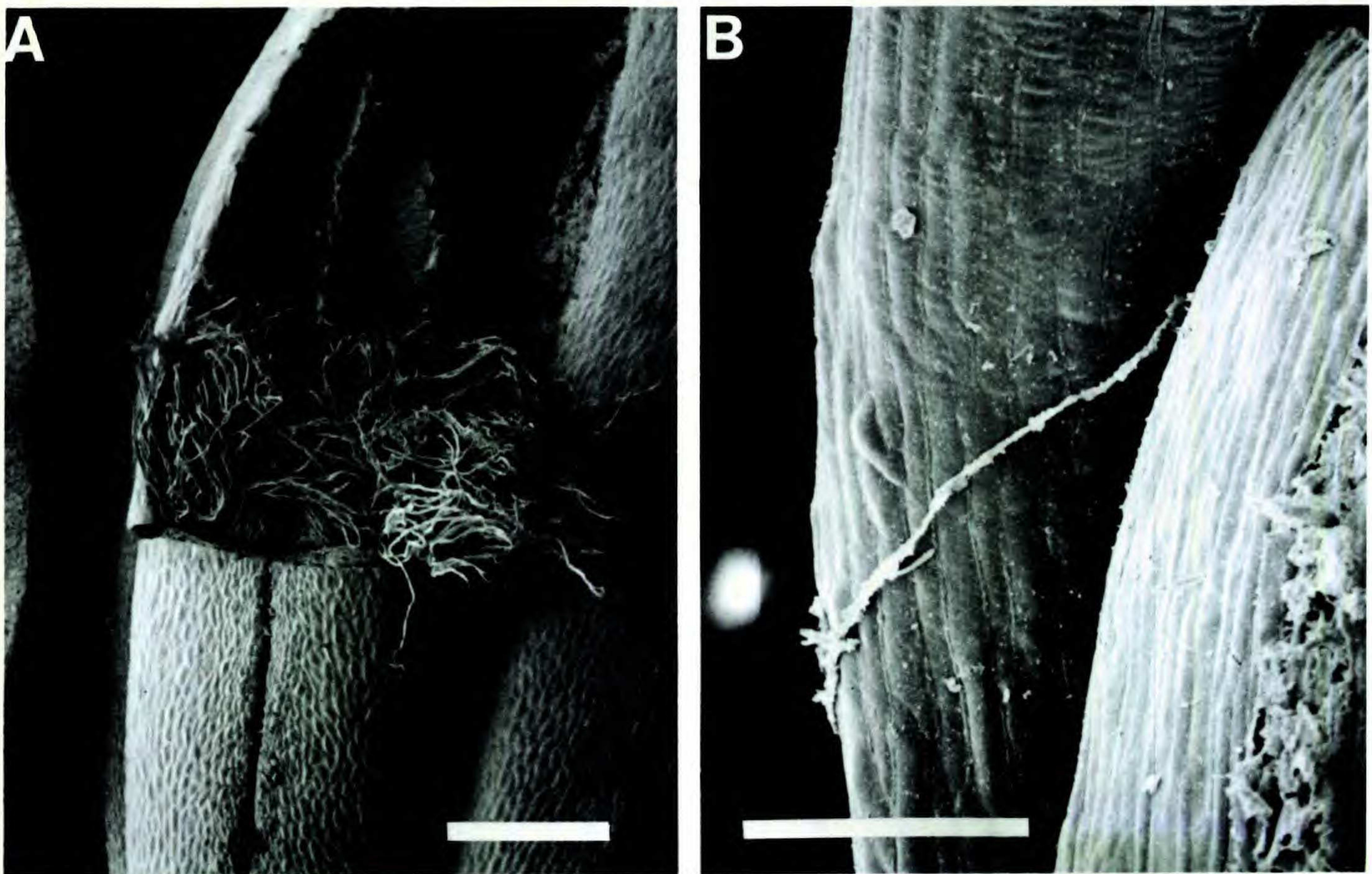
FIGURE 2.   *Reproductive structures of* Amphibolis antarctica.—*A. Staminate floral unit prior to dehiscence, with the filiform pollen exposed (scale = 1 mm).*—B. Filiform pollen grain on an Amphibolis *stigma from a natural pollination event in the Point Lonsdale, Victoria, population (scale = 100 µm).*

cluded on the basis of our current observations and may also occur in the species.

The floral morphology of *A. antarctica* permits only one of the two sets of stigmas in each pistillate floral unit to encounter the water surface and hence be pollinated. This may relate to the fact that only one of the two ovaries develops, while the other one aborts (Tomlinson, 1982). This condition is analogous to the situation in *Ruppia*, where the inflorescence frequently floats on the surface in such a way that only one of the sets of stigmas is exposed to floating pollen while the other is submerged. Germination in *A. antarctica* is viviparous (Fig. 3F) (Black, 1913), with the mature seedling being released together with an unvascularized "grappling apparatus" (Fig. 3G) that develops as an outgrowth of the female floral unit (McConchie et al., 1982). This grappling apparatus presumably assists in attaching the seedling to a substrate.

SEARCH VEHICLE SIZE AND SUCCESS in *RUPPIA SPIRALIS*

Although two-dimensional search theory predicts that large search vehicles are much more likely to encounter stigmas than small search vehicles (Cox, 1983b), there has yet to be an empirical test of this prediction. We therefore studied pollen/stigma encounters in a *Ruppia maritima*

population growing in a brackish pond near Queenscliff, Victoria. Using an immersible camera stand, we filmed natural pollination events with a video camera equipped with a macro lens. The video tape was then analyzed frame by frame with a high-resolution freeze-frame video deck attached to a Zeiss Videoplan digital imaging system. Dimensions of all search vehicles were calculated by digitizing their images on the video screen. The size distributions (largest diameters) of 1,000 such search vehicles chosen at random from the video footage were calculated and recorded. Then the video tape was analyzed again to determine the sizes of search vehicles that actually collided with stigmas. This was accomplished by finding a frame in which a search vehicle could be seen to hit the stigma, and then reversing the tape several frames so that the dimensions of the search vehicle prior to collision could be determined. This procedure was repeated for 100 such search vehicles.

The respective size distributions of successful search vehicles together with the size distributions of all search vehicles are shown in Figure 4. The median size of all search vehicles was found to be 812 µm (N = 1,000), while the median size of successful search vehicles was much larger (1,388 µm; N = 100). A U-test for the difference between the medians was significant at the 0.05 level. This
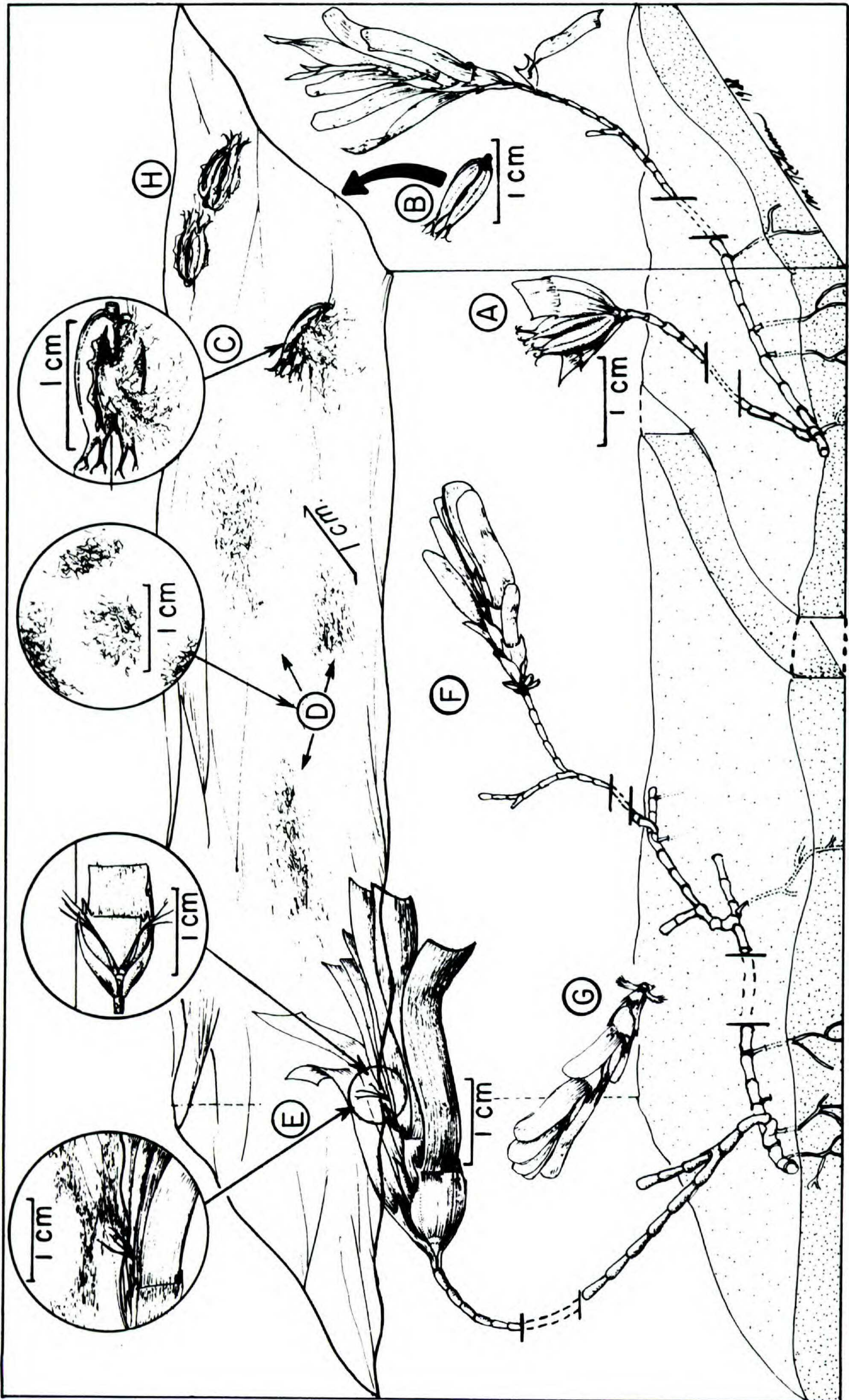
FIGURE 3. Pollination of *Amphibolis antarctica* in an intertidal population at Point Lonsdale, Victoria, Australia.—A. Staminate plant with staminate floral unit prior to abscission.—B. Abscised staminate floral unit floating to surface.—C. Abscised staminate floral unit at dehiscence, releasing cottony mass of pollen.—D. Fractallike search vehicles of A. antarctica pollen floating on surface of sea.—E. Top of pistillate plant floating on water surface with plane of distichous phyllotaxy coplanar with water surface. Note styles protruding from water surface. Upper left insert illustrates contact of search vehicle with stigmas.—F. Vivparous seedling growing on maternal parent.—G. Dispersal of abscised seedling.
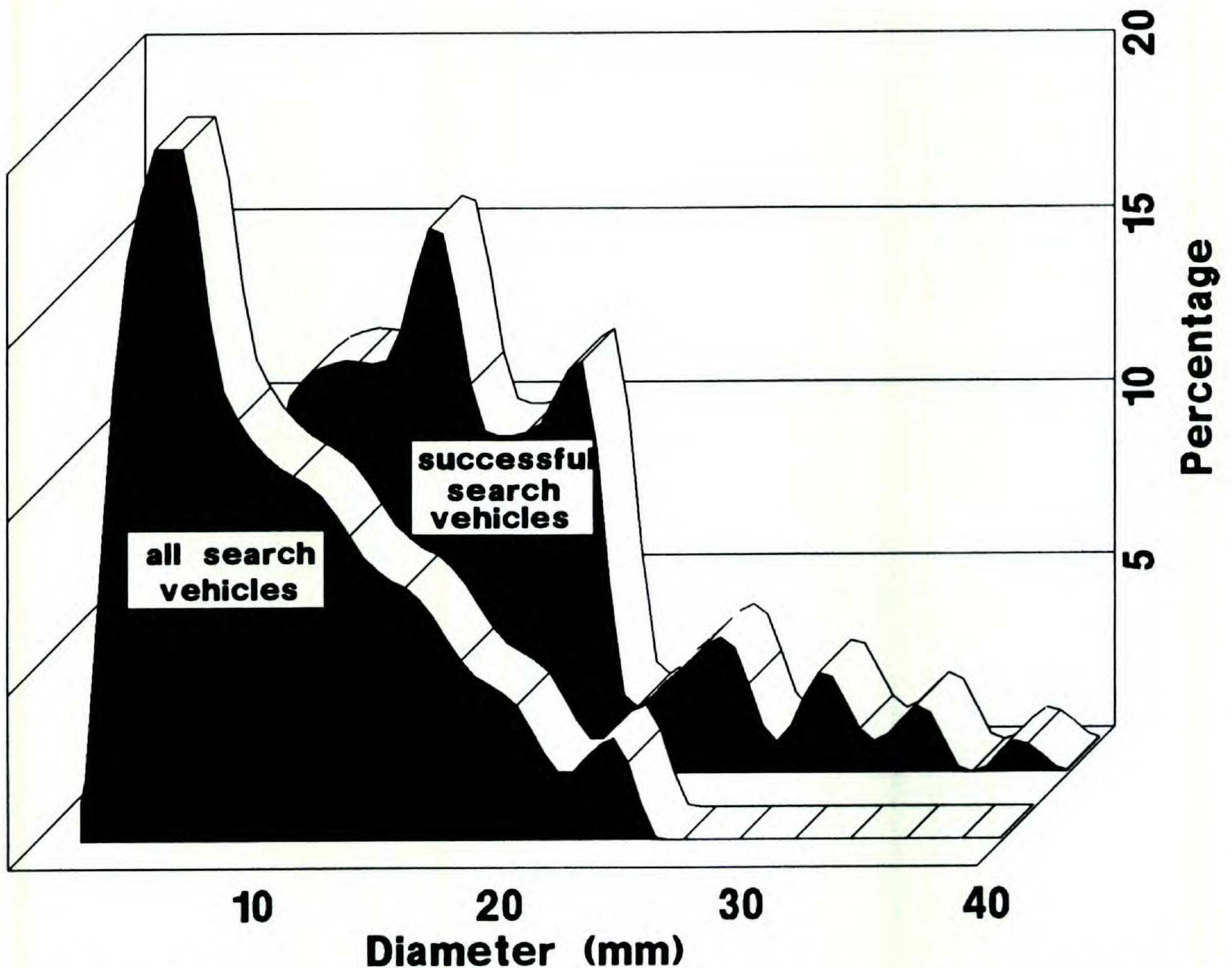
FIGURE 4. *Size distributions of* Ruppia spiralis *search vehicles filmed near Queenscliff, Victoria. The distribution labeled "all search vehicles" represents the size distribution of 1,000 search vehicles chosen at random, while the distribution labeled "successful search vehicles" represents the size distribution of 100 search vehicles that collided with stigmas.*

suggests that larger search vehicles do, in accordance with theoretical predictions, have a much greater chance of successfully encountering a stigma than small search vehicles.

Many questions, however, remain concerning two-dimensional pollination. What is the role of stigma morphology on search vehicle encounter rates? Computer simulations (P. A. Cox & J. Sethian, unpubl. data) indicate filamentous stigmas to be far more efficient in pollen capture, but the relative importance of stigmatic texture is unknown. The stigmas of the five surface-pollinated genera we studied are smooth, while the stigmas of the two-dimensional submarine-pollinated species *Thalassia testudinum* are densely papillate (Cox & Tomlinson, 1988). Major questions also remain concerning mixed modes of pollination. Is it possible that some seagrasses have both surface and submarine modes of pollination as has been suggested by Hartog (1970) for *Phyllospadix* and *Zostera* (Cock, 1980)? If so, what are the relative impor-

tances of these different modes? Another important question concerns the effect of two-dimensional pollination systems on breeding systems. If the pollen shadows are far smaller than the average clone size of the species, will there be strong selection for obligate outbreeding systems (Cox, 1988) such as dioecism? It is of interest in this regard that 75% of the seagrass genera are dioecious. Gene flow between populations mediated by pollen exchange must be exceedingly rare in seagrasses (Cox, 1983b) and even rarer in freshwater hydrophilous plants, since the pollen cannot move from one pond to another (Cook, 1987). The evolutionary ecology of such genetically isolated populations merits further investigation. Finally, convincing evolutionary explanations have yet to be made of lack of a developed exine in the pollen of many hydrophilous plants (Ducker et al., 1978). We believe that more light will be shed on these questions as further ecological studies are made of two-dimensional pollination systems.

LITERATURE CITED

ASTON, H. I. 1973. Aquatic Plants of Australia. Melbourne Univ. Press, Carlton, Victoria.

BLACK, J. M. 1913. The flowering and fruiting of *Pectinella antarctica* (*Cymodocea antarctica*). Trans. Roy. Soc. Australia 37: 1–5.

BROCK, T. D. 1966. Principles of Microbial Ecology. Prentice Hall, Englewood Cliffs, New Jersey.

COCK, A. W. A. M. DE. 1980. Flowering, pollination, and fruiting in *Zostera marina* L. Aquatic Bot. 9: 209–220.

COOK, C. D. K. 1982. Pollination mechanisms in the Hydrocharitaceae. Pp. 1–15 *in* J. J. Symoens, S. S. Hooper & P. Compère (editors), Studies on Aquatic Vascular Plants. Royal Botanical Society of Belgium, Brussels.

———. 1987. Vegetative growth and genetic mobility in some aquatic weeds. Pp. 217–225 *in* K. M. Urbanska (editor), Differentiation Patterns in Higher Plants. Academic Press, London.

COX, P. A. 1981. Vertebrate Pollination and the Maintenance of Unisexuality in *Freycinetia*. Ph.D. Dissertation. Harvard University, Cambridge, Massachusetts.

———. 1983a. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, *Freycinetia arborea*. Oikos 41: 195–199.

———. 1983b. Search theory, random motion, and the convergent evolution of pollen and spore morphologies in aquatic plants. Amer. Naturalist 121: 9–31.

———. 1984. Chiropterophily and ornithophily in *Freycinetia* in Samoa. Pl. Syst. Evol. 144: 277–290.

———. 1988. Monomorphic and dimorphic sexual strategies: a modular approach. Pp. 80–97 *in* J. Lovett Doust & L. Lovett Doust (editors), Plant Reproductive Ecology: Strategies and Patterns. Oxford Univ. Press, Oxford.

———. Hydrophilous pollination. Ann. Rev. Ecol. Syst. (in press).

——— & R. B. KNOX. 1986. Pollination postulates and two-dimensional pollination. Pp. 48–57 *in* E. G. Williams, R. B. Knox & D. Irvine (editors), Pollination '86. Univ. Melbourne Press, Melbourne.

——— & ———. Two-dimensional pollination in hydrophilous plants: convergent evolution in the genera *Halodule* (Cymodoceaceae), *Halophila* (Hydrocharitaceae), *Ruppia* (Ruppiaceae), and *Lepilaena* (Zannichelliaceae). Amer. J. Bot. (in press).

——— & P. B. TOMLINSON. 1988. The pollination ecology of a Caribbean seagrass, *Thalassia testudinum* (Hydrocharitaceae). Amer. J. Bot. 75: 958–965.

DEGENER, O. 1930. Plants of Hawaii National Park. Braun-Brumfield, Ann Arbor, Michigan.

DE KRUIF, P. 1927. Microbe Hunters. Latimer, Whilstable.

DUCKER, S. C., N. J. FOORD & R. B. KNOX. 1977. Biology of Australian seagrasses: the genus *Amphibolis* C. Agardh (Cymodoceaceae). Austral. J. Bot. 25: 67–95.

———, J. M. PETTITT & R. B. KNOX. 1978. Biology of Australian seagrasses: pollen development and submarine pollination in *Amphibolis antarctica* and *Thalassodendron ciliatum* (Cymodoceaceae). Austral. J. Bot. 26: 265–285.

ERNST-SCHWARZENBACH, M. 1945. Zur Blütenbiologie einiger Hydrocharitaceen. Ber. Schweiz. Bot. Ges. 55: 33–69.

FAEGRI, K. & L. VAN DER PIJL. 1979. The Principles of Pollination Ecology, 3rd edition. Pergamon, Oxford.

GAMERRO, J. C. 1968. Observaciones sobre la biología floral y morfología de la Potamogetonacea *Ruppia cirrhosa* (Petag.) Grande (= *R. spiralis* L. ex Dum.). Darwiniana 14: 575–608.

HARPER, J. L. 1978. Population Biology of Plants. Academic Press, London.

HARTOG, C. DEN. 1970. The Sea-Grasses of the World. Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 59. North Holland, Amsterdam.

HERSCH, R. & R. J. GRIEGO. 1969. Brownian motion and potential theory. Sci. Amer. 220(3):66–74.

JENNINGS, J. D. 1979. The Prehistory of Polynesia. Harvard Univ. Press, Cambridge, Massachusetts.

KOCH, R. 1880. Investigations into the Etiology of Traumatic Infectious Diseases. Translated by W. W. Cheyne. The Sydenham Society, London.

KOOPMAN, B. O. 1956. The theory of search. II: Target detection. Operations Res. 4: 503–531.

McCONCHIE, C. A., S. C. DUCKER & R. B. KNOX. 1982. Biology of Australian seagrasses: floral development and morphology in *Amphibolis* (Cymodoceaceae). Austral. J. Bot. 30: 251–264.

McMILLAN, C. 1980. Flowering under controlled conditions by *Cymodocea serrulata*, *Halophila stipulacea*, *Syringodium isoetifolium*, *Zostera capensis* and *Thalassia hemprichii* from Kenya. Aquatic Bot. 8: 323–336.

PETTITT, J. M. 1980. Reproduction in seagrasses: nature of the pollen and receptive surface of the stigma in the Hydrocharitaceae. Ann. Bot. (London) 45: 257–271.

———. 1981. Reproduction in seagrasses: pollen development in *Thalassia hemprichii*, *Halophila stipulacea* and *Thalassodendron ciliatum*. Ann. Bot. (London) 48: 609–622.

———, S. C. DUCKER & R. B. KNOX. 1981. Submarine pollination. Sci. Amer. 244: 134–143.

———, C. A. McCONCHIE, S. C. DUCKER & R. B. KNOX. 1980. Unique adaptations for submarine pollination in seagrasses. Nature 286: 487–489.

———, ———, ——— & ———. 1983. Reproduction in seagrasses: pollination in *Amphibolis antarctica*. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 219: 119–135.

PROCTOR, M. & P. YEO. 1973. The Pollination of Flowers. Collins, London.

TOMLINSON, P. B. 1982. Anatomy of the Monocotyledons. VII. Helobiae (Alismatidae) (Including the Seagrasses). Clarendon Press, Oxford.

TROLL, W. 1931. Botanische Mitteilungen aus den Tropen II. Zur Morphologie und Biologie von *Enhalus acoroides* (Linn. f.) Rich. Flora 125: 427–456.

VAN VIERSSEN, W. R. J. VAN WIJK & J. R. VAN DER ZEE. 1982. On the pollination mechanism of some eurysaline Potamogetonaceae. Aquatic Bot. 14: 339–347.

VERHOEVEN, J. T. A. 1979. The ecology of *Ruppia*-dominated communities in Western Europe. I. Distribution of *Ruppia* representatives in relation to their autecology. Aquatic Bot. 6: 197–268.

WYLIE, R. B. 1917. The pollination of *Vallisneria spiralis*. Bot. Gaz. (Crawfordsville) 63: 135–145.